

Comment on temperature-dependent stock–recruit modeling for Pacific sardine (*Sardinops sagax*) in Jacobson and MacCall (1995), McClatchie et al. (2010), and Lindegren and Checkley (2013)

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Jacobson and MacCall (1995, JM) estimated spawner–recruit models for the northern stock of Pacific sardine (*Sardinops sagax*) along the western coast of North America with log recruitment and log recruitment success as the dependent variables. Log recruitment models are the topic of this comment and most important for Pacific sardine. JM used data ($N = 34$) for 1935–1963 and 1985–1990 (Fig. 1). Their preferred log recruitment model included a statistically significant nonlinear relationship with spawning biomass and a statistically significant linear relationship with three season average sea surface temperature data collected at Scripps Pier (SPSST) in San Diego, California.

McClatchie et al. (2010, MEA) reevaluated the spawner–recruit relationship for Pacific sardine using additional data for 1991–2008 (Fig. 1). They found a statistically significant relationship between spawning biomass and log recruitment. However, the relationship with SPSST “broke down” when additional data were included. Loss of statistical significance as data accumulate is a common and important problem in modeling recruitment using environmental variables (Myers 1998).

Lindegren and Checkley (2013, LC) revisited the question of temperature effects on Pacific sardine recruitment using a shorter but more recent set of spawning biomass and recruitment data (1981–2010) and annual (rather than three-season average) environmental indices. LC’s environmental data included SPSST, mean sea surface temperatures at 5–15 m measured in the Southern California Bight spawning habitat during California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises, and several other candidate data sets. LC did not use data for 1935–1965 because spawning biomass and recruitment estimates used as data for 1981–2010 could be obtained from a single assessment model source (JM and MEA used data from several sources). LC found that annual SPSST data were statistically significant although SST at 5–15 m from CalCOFI cruises was a better predictor for log recruitment and log recruitment success. CalCOFI SST data were used in their best models. Apart from using different data sets, LC did not explain differences in results from the three studies beyond pointing out the different modeling approaches in MEA and LC. The explanation is a main goal our comment.

Uncertainty about on-and-off-again temperature effects on Pacific sardine recruitment is important. Myers (1998) identified Pacific sardine as one of only two cases in which environment–recruitment relationships had held up with the passage of time and were used in stock assessment work. JM’s results were used to

help predict recruitments in stock assessment modeling during 1996 to 2003 when analysts switched to stock assessment programs that did not accommodate environmental effects on recruitment. The Pacific Fishery Management Council adopted an SPSST-dependent environmental control rule for Pacific sardine with maximum harvest rates varying from 5% under cool conditions to 15% under warm conditions based on JM’s findings. The control rule was used until MEA published their results (Pacific Fishery Management Council 1998). Based on a stock assessment finalized in 2011 (Hill et al. 2011) and MEA’s results, SPSST-dependent control rule was abandoned and the Pacific Fishery Management Council’s Science and Statistical Committee concluded that “... temperature, or another correlated environmental variable, may be important in sardine recruitment, but that the SIO [SPSST] index is not reflective of the temperature in the area of greatest sardine spawning activity and is no longer correlated with sardine productivity.” (Pacific Fishery Management Council 2011). MEA’s results and lack of an explanation for different conclusions among JM, MEA, and LC caused considerable uncertainty and controversy about environmental effects on recruitment of Pacific sardine.

After reconsidering methods and reanalyzing MEA’s data, we determined that their models suffered from statistical shortcomings that caused misleading results. In particular, MEA fit log recruitment and other models by linear regression in two steps. In the first step, log recruitment was regressed on spawning biomass, and the p value for spawning biomass was calculated from the results of the first regression. In the second step, residuals from step one were regressed on SPSST, and the p value for SPSST was calculated from the results of the second regression.

The intent of MEA’s modeling approach was to remove density-dependent effects before estimating environmental effects. However, sequential regression on residuals gives incorrect parameter estimates, p values, and other results when the predictor variables are correlated (the correlation between spawning biomass and SPSST data used by MEA was $\rho = -0.23$). Weisberg (1980, pp. 35–40) gives a clear demonstration of this problem in multiple regression analysis, and it is straightforward to show by simulation that a correlation of $\rho = -0.23$ is sufficient to undermine statistical results. This problem occurs because the relative importance of spawning biomass and SPSST in predicting recruitment is obscured to the extent that the predictor variables S and T are cor-

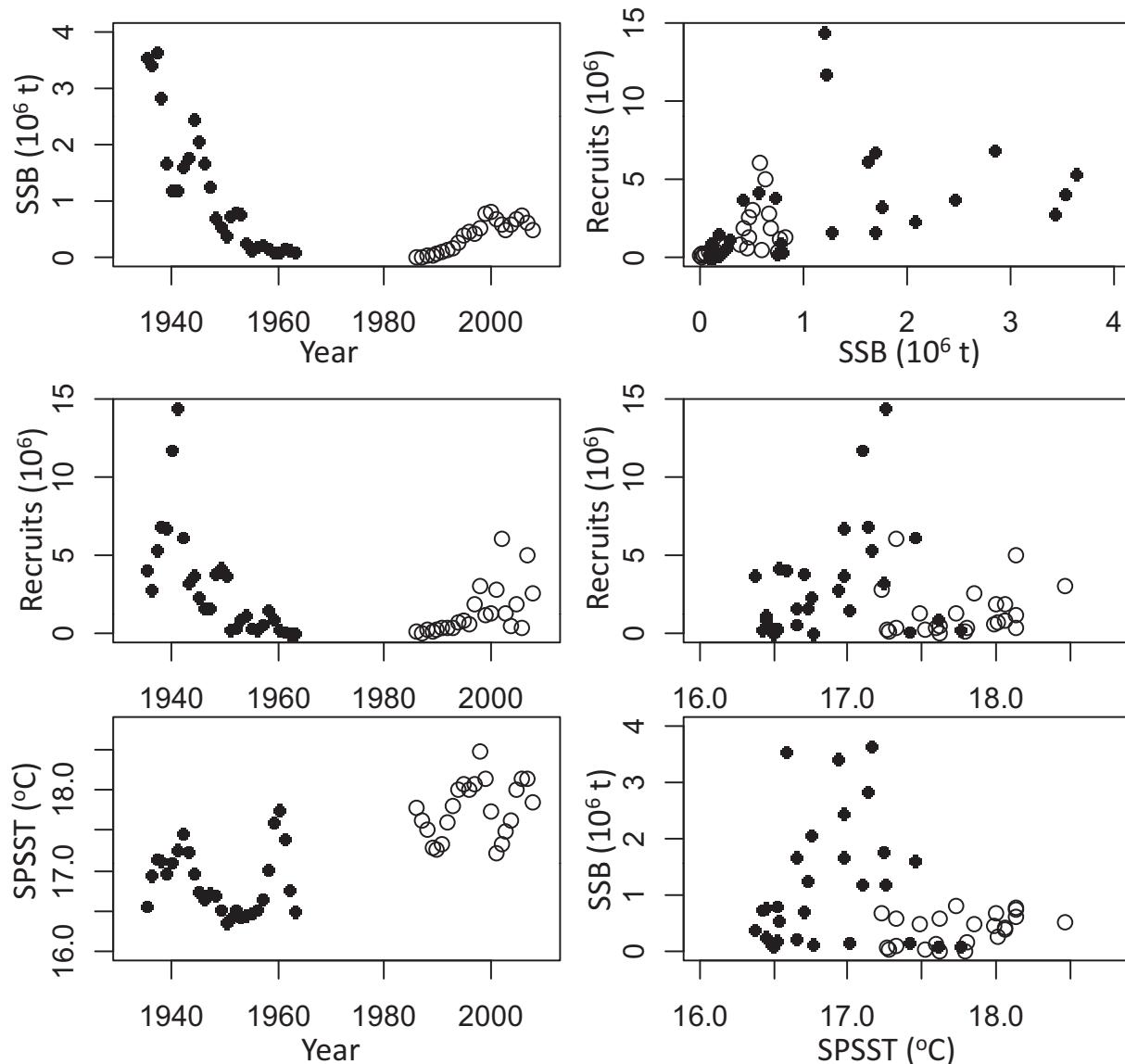
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Fig. 1. Recruitment (numbers at age 2), spawning biomass (SSB), and 3-year average Scripps Pier sea surface temperature (SPSST) data for Pacific sardine. Solid symbols are for historical data (1935–1963), and open symbols are for recent data (1985–2008). Jacobson and MacCall (1995) used data through 1990, while McClatchie et al. (2010) used all of the data shown.



related. The correct and common approach is to fit both predictor variables simultaneously in the same model and estimate uncertainty about main and joint effects in terms of the variance and covariance of the parameter estimates. The correct approach does not remove uncertainty about correlated predictors, but it does result in best-fit maximum likelihood estimates.

To better understand differences among studies, we reanalyzed MEA's data using standard maximum likelihood model fitting techniques, a family of models that includes both linear and nonlinear forms, and standard model selection criteria (Wood 2006). The generalized version of JM's log recruitment model used in this analysis is

$$(1) \quad \ln(R) = \alpha + g(S) + h(T) + \varepsilon$$

where α is an estimated intercept parameter, R is recruitment (10^6 fish) at age 2 years, S is spawning biomass (10^3 t), T is mean three-season SPSST ($^{\circ}\text{C}$), and ε is a lognormal statistical error. The

terms $g(S)$ and $h(T)$ are smooth nonlinear tensor product functions that are estimated in the model (Wood 2006). JM used loess smoothers and LC used thin-plate smooth functions in place of tensor product functions, but this had little effect on results.

MEA's linear model was

$$(2) \quad \ln(R) = \alpha + \beta T + \gamma S + \varepsilon$$

where β and γ were estimated parameters. In addition to model (1), we used the single term models:

$$(3) \quad \ln(R) = \alpha + g(S) + \varepsilon$$

$$(4) \quad \ln(R) = \alpha + h(T) + \varepsilon$$

and the null model:

$$(5) \quad \ln(R) = \alpha + \varepsilon$$

Table 1. Stock–recruit modeling results for Pacific sardine with and without SPSST effects (sorted by AIC).

Model description	Model No.	df	AIC	Tested against	p value
Null	4	1	187	—	—
GAM, SPSST only	3	5.2	184	4	0.021
Linear, spawning biomass and SPSST	5	3	167	—	—
GAM, spawning biomass only	2	5.7	142	4	<10 ⁻¹⁵
GAM, spawning biomass and SPSST	1	8.8	138	2	0.029

Note: “df” is degrees of freedom for linear plus nonlinear terms in the model. “Tested against” and “p value” refer to nested model numbers and likelihood ratio tests. For example, model (3) was tested against the simpler model (4), and SPSST was significant at $p = 0.021$. The linear model (5) is analogous to McClatchie et al.’s (2010) model and was not included in likelihood ratio tests because it is a special case of model (1). SPSST, sea surface temperature data collected at Scripps Pier; AIC, Akaike’s information criterion; GAM, generalized additive model.

in statistical comparisons. Models (2) to (5) are special cases of model (1) because the tensor product functions in generalized additive models (GAMs) tend to straight lines as in linear regression if there is little statistical evidence for a nonlinear relationship and because they tend towards straight horizontal lines (slope = 0) when there is little evidence of any linear relationship (Wood 2006).

We fit models (1) to (5) as GAMs using mgcv library software in the R programming language (Wood 2006; R Development Core Team 2008). The amount of curvature in the tensor product functions was determined during model fitting using a built-in procedure based on Akaike information criteria (AIC) statistics. LC used a similar approach but limited the overall flexibility of nonlinear terms. JM selected the amount of curvature by eye based on residual patterns. We used likelihood ratio tests for nested models as well as AIC statistics to help select the best model in our reanalysis.

As in all three previous studies, spawning biomass was highly significant ($p < 10^{-15}$) and the most important single predictor of log recruitment in GAMs (Table 1; Fig. 2). SPSST was also statistically significant ($p = 0.029$), and model (1) was selected as the best model overall based on likelihood ratio and AIC statistics. The estimated relationships among recruitment, spawning biomass, and SPSST were nonlinear, and there were no pathological patterns in plots of likelihood residuals versus predicted values, spawning biomass, and SPSST.

As in LC, cross validation results showed that the best model was useful for predicting recruitments not included in the original model fit (Picard and Cook 1984). In cross-validation, each observation in the original data set was excluded sequentially, the model was fit to the remaining data, and the fitted model was used to predict the excluded data point. The R^2 statistic was 58% for omitted observations compared with $R^2 = 71\%$ for the original model fit to all of the data. In- and out-of-sample predictions for log recruitment were highly correlated ($\rho = 0.91$). These results are like the cross-validation results in LC and indicate that our conclusions about predicting new recruitments are robust and not due to using a particular data set or a “lucky” model.

Simulations were used to evaluate statistical power and probability of a type 1 error with autocorrelated errors in recruitment and various levels of correlation between the true environmental factor controlling recruitment and SPSST (see online Supplemental Material¹). Type 1 error rates for SPSST were $\leq 25\%$ if p values for likelihood ratio tests were ≤ 0.05 . Statistical power in detecting an SPSST effect was 0.56 at $p = 0.05$ with perfect correlation between SPSST data and the causative environmental factor in simulations. When SPSST was only correlated with the causative factor, statis-

tical power was reduced but always at least 0.16. JM carried out similar simulations with autocorrelated errors and reached similar conclusions. Given both sets of simulation results and general similarities among models in the three studies, it seems likely that conclusions about environmental effects on sardine recruitment are not unduly influenced by autocorrelation in residuals. In addition, the fact that SPSST effects were detected may indicate that the correlation between SPSST and underlying causative factor is relatively high.

The most important conclusion from our reanalysis is affirmation that spawning biomass and SST effects on Pacific sardine recruitment appear relatively strong and consistently detectable using spawning biomass and recruit data from various sources and at least two sources of SST data. Moreover, cross-validation results indicate that models used to reach this conclusion appear reasonably reliable and stable.

We do not advocate SPSST as an alternative to the CalCOFI SST data source used by LC. Further progress is inevitable, but we support LC’s analysis and use of CalCOFI SST because of the high predictive power and stability of their models, use of annual data rather than relatively long three-season averages (which are hard to justify), use of SST data from spawning grounds, and because of the consistent source of their spawning biomass and recruit data. One important characteristic of LC’s data is that their SST and spawning biomass data are uncorrelated, making it easier to distinguish between spawning biomass and SST effects on Pacific sardine recruitment.

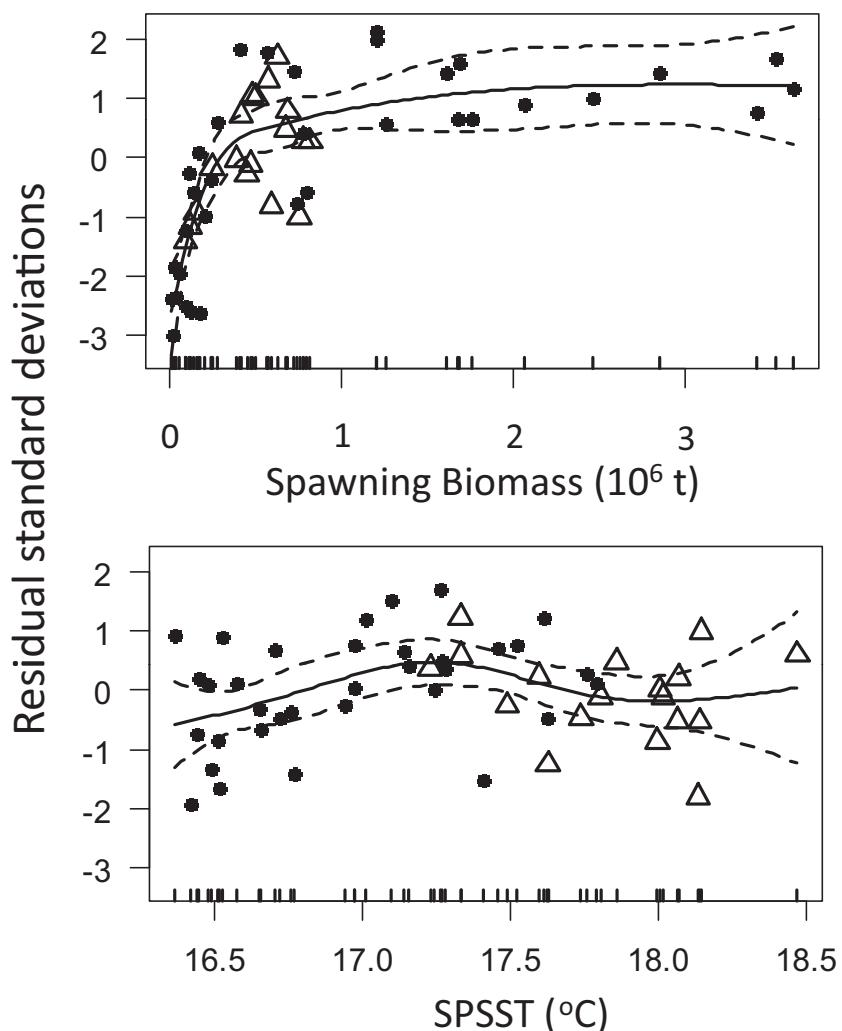
With all of the interest in environmental effects, it is important to remember that spawning biomass (density-dependent effects) was more important than SST in predicting Pacific sardine recruitment in all of the studies mentioned here. This commonality and the management strategy oriented simulations in Pacific Fishery Management Council (1998) indicate that fishery managers should try to maintain adequate levels of spawning biomass while adjusting expectations for potential recruitment or reference points based on environmental data.

Future research should update JM by estimating relationships among maximum sustained yield reference points, spawning biomass, and the environment using updated methods and data. New management strategy analyses are already underway.² It would be useful in future research to obtain spawning biomass and recruitment estimates for Pacific sardine back to the early 1930s so that a consistent set of data for the entire history of the fishery could be used to study environmental effects.

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0128>.

²Report of the Pacific sardine harvest parameters workshop, 5–13 February 2013. Pacific Fishery Management Council, Portland, Ore.

Fig. 2. Model (1) fit to log recruitment, spawning biomass, and SPSST data for Pacific sardine with approximate 95% confidence intervals (dashed lines) for the fitted solid line. Solid circles show partial residuals from the fit to data for 1935–1990. Open triangles show partial residuals from the fit to data for 1991–2008.



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